VII. *On some Points in the Morphology and Anatomy of the* Nymphæaceæ. *By* D. T. GWYNNE-VAUGHAN, *B.A. Cantab.* (*Communicated by* D. H. SCOTT, *F.R.S.*, *F.L.S.*, *Hon. Keeper of the Jodrell Laboratory, Royal Gardens, Kew.*)

(Plates XXI. & XXII.)

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Morphology of the Leaf.

SOME time ago the rhizome of a mature plant of *Victoria regia* and also a number of young seedlings of the same which had been grown in the Royal Gardens, Kew, were placed in my hands; and I spent some time under the direction of Dr. Scott, for whose valuable advice and supervision throughout I have every reason to be grateful, in examining the material thus placed at my disposal. In the course of this examination various points of such interest came into view as to lead to the investigation of other plants of the same order for the sake of comparison. Some of the results obtained thereby I have ventured to detail in this paper.

In dissecting away the growing-point of the mature rhizome some of the earliest stages of the adult leaves were disclosed, and since I have not met with any figures of the well-known leaf in its young state, three of them are represented on an enlarged scale in Pl. XXI. figs. 1, 2, & 3.

The smallest leaf figured is about 1·5 mm. long; and here it may be seen that the rudimentary lamina stands erect and broadly based on a short, stout support, the future petiole, the extension of the lamina below the point of insertion being much less than the extension above it. So the petiole is inserted excentrically, and the general outline of the lamina is ovate and not orbicular. The sides of the lamina are raised up like those of a bowl, the edges being rounded off owing to the fact that they are slightly curled inwards, although the involute prefoliation which is a characteristic of the young leaf in its later stages is not nearly so prominent in the earlier ones.

The apex tapers to a blunt point slightly incurved, and differing but little, if at all, in texture or appearance from the rest of the leaf—quite otherwise than what might be expected from the case of *Euryale ferox*. Judging from a plate of that plant given in the 'Flore des Serres et des Jardins de l'Europe,' illustrating a description written by Planchon, the general appearance of an early stage of an adult leaf is closely similar to that described for *Victoria regia*; on the other hand, the apex takes the form of a broad terminal lobe folded over on to the ventral surface like a hood, being almost free from prickles, and not partaking in the involution of the rest of the leaf.

In view of the suggestion put forward by Baillon with regard to the differentiation of the pitchers of *Sarracenia*, *Nepenthes*, &c., that they were derived by an extreme

exaggeration of the peltation of such a bowl-shaped peltate lamina as that of *Nelumbium*, the operculum representing a portion of the lamina unaffected by the peltation, this hood or terminal lobe of the young *Euryale* leaf might well be compared with the operculum of a pitcher. The great similarity between the early development of the pitchers and of peltate leaves, such as those of *Victoria* and *Nelumbium*, also tends to show that a comparison between the two is not altogether fanciful.

The methods of origin of a pitcher on the one hand, and of a peltate lamina on the other, as respectively described by Bower * and Trécul † are fundamentally identical. The first indication of each is the appearance of a shallow depression on the adaxial side of the leaf-rudiment, just below its apex; which depression is caused by the slow growth of a central area relative to that of the regions surrounding it. A single point of difference is that in *Nelumbium* the growth of the region at the base across the summit of the petiole is for a time delayed, so that, to begin with, the central depression is but incompletely surrounded by a horseshoe-shaped emergence instead of a complete annular cushion. However, the delayed region soon takes up a more rapid growth, joining the two arms of the horseshoe transversely across the summit of the petiole; then the whole grows out into the peltate lamina.

Prof. Bower has shown (*l. c.*) that the operculum of the pitcher is at first a two-lobed structure, which he regards as representing two pinnæ congenitally coalescent across the adaxial surface of the leaf. It is known that in certain peltate leaves, as in *Hydrocotyle vulgaris* ‡ and in *Tropæolum majus* (Trécul, *l. c.*), the earlier stages are seen to be very distinctly lobed with a terminal unpaired lobe. With this fact in view, it becomes easy to suppose that in the pitchers, themselves originating in a lobed leaf-rudiment, the upper pair of lobes may remain free from the peltation of the rest of the leaf, to form an operculum in the manner described by Prof. Bower, while the terminal lobe grows out into the spur found at the point of the insertion of the operculum on to the pitcher on the dorsal side.

The prickles and spines which beset the under surface of the adult leaves of *Victoria regia* are also clearly visible on young leaves which have attained a length of about 5 mm. Before that size is reached, although the petiole and the lamina with its principal veins are already clearly developed, the prickles are not yet visible. They first make their appearance as little rounded projections on or near the midrib, at the points where the lateral veins join on to it, the midrib being at this stage by far the principal vein in the leaf. Most of the larger prickles are traversed by a narrow strand of vascular tissue, and they are said by Trécul § to terminate in a "pore" or "ostiole" which opens below into a small cavity. My observations, however, entirely confirm those of Mr. Blake (Ann. Bot., i. p. 74), who failed to find any trace of this pore. I noticed, however, that if the tip of one of these prickles be viewed directly from above, the rounded terminations of a number of cells which are arranged in a ring around a central one give an appearance

* Ann. of Bot., vol. iii. p. 239.

† Ann. des Sc. Nat., sér. 3, vol. xx. p. 261.

‡ Goebel, Schenk's 'Handbuch der Bot.,' Band iii. 1ste Hälfte, p. 234.

§ Ann. des Sc. Nat., sér. 4, tom. i. p. 156.

not unlike that figured by Trécul; and in the absence of any sections of the prickle may have led him to look upon it as bearing an actual pore.

Van Tieghem considers the prickles to be homologous with those on the surface of the leaves of certain varieties of *Ilex Aquifolium*, or with the tentacles of *Drosera*.

The method of growth of the leaves of *Victoria regia* has been fully described by Planchon in his monograph on this plant, although he gives no figures attached.

At the base of each mature leaf on its ventral side there lies a membranous scale, curving away from the leaf to which it belongs, and sheathing all the younger structures in the bud (Pl. XXI. fig. 4). It is formed by the fusion of two stipules along their inner margins on the adaxial side of the leaf. The first or first two leaves of the seedling have no such axillary scale, but their bases are slightly winged by two small lateral appendages, which probably represent the free lateral stipules found in certain Nymphæas, *N. zanzibariensis* &c. (fig. 5). The intrafoliar scale of *Nelumbium* is probably derived in the same way as that of *Victoria*.

The embryonic leaves of the seedling are quite different in appearance from the adult leaves of the mature plant, and they show, by an interesting series of gradations, a progressive change from an acicular primordial leaf (or petiole only, according to Trécul) to the peltate form of the mature plant. The exact form of corresponding leaves in different seedlings varies considerably. However, the first leaf is always found to be acicular. The second possesses a lamina, usually elongate-lanceolate, sometimes with two small hastate lobes at the base. The third (fig. 6) varies from elongate-hastate to deltoid-hastate, the auricles are widely divergent, and at the base of the lamina, just above the insertion of the petiole, there is invariably a little pocket or pouch on its adaxial side, which appears to have been formed by the fusion of the auricles at their bases across the adaxial surface of the leaf. The fourth (figs. 7 & 8) is the first that bears spines, and that shows itself to be distinctly peltate. It is the first swimming leaf, and has a lamina oval in outline with a subacute apex; there are two auricles at the base which do not diverge, but lie more or less close together, thus making the leaf sagittate. The fusion between them at their bases is here carried much further than in the previous leaf; in fact, they are fused together for about a third of their whole length from the point of insertion of the petiole, the line of fusion being followed by a small vein. So the final form attained by this leaf closely resembles that of the adult leaves of many Nymphæas, *N. Lotus, gracilis, delicatissima*, &c., in which the fusion of the auricles is never carried any further. In *Victoria regia*, on the other hand, the succeeding leaves become more and more orbicular in outline, and the auricles become fused along a successively greater part of their length until the final form of the adult leaf is attained.

As previously stated, the leaf of the mature plant owes its peltation to the formation of a zone of growth across the summit of the petiole on the adaxial surface of the leaf, which by its activity forms a mass of tissue joining together two parts of the lamina previously separate and distinct. Hence it would appear that the leaf of the mature plant passes in its youth through stages which are quite parallel to those permanently retained by the embryonic leaves. Thus, the third leaf of the embryo may be regarded

as the first in which the transverse zone appears at all; its activity being as yet but little marked, the structure arising from it is correspondingly minute. Whereas in the fourth and succeeding leaves the duration of its activity and the results obtained thereby become more and more considerable. So, in this case at least, it may be said that the ontogeny, if it may be so termed, of a single leaf of the mature plant repeats, in some degree at any rate, the true ontogeny of the leaves of the plant as a whole—that is to say, it repeats the developmental stages of the embryo.

The embryonic leaves of *Nymphæa* and *Nuphar* pass through a series of stages somewhat similar to those of *Victoria* until a more or less sagittate form is reached. In many species no further advance is made, the auricles remaining practically free throughout (*Nymphæa pygmæa*, *N. stellata*). In others (those mentioned above) they fuse together to about the same extent as they do in the fourth leaf of *Victoria*.

The adult leaves of *Barclaya* show a still simpler form, being elongate, strap-shaped, and slightly auricled. After consideration of the above gradations they might perhaps be held as approximating to the ancestral leaves of the *Nymphæaceæ* in their form.

With regard to its embryonic leaves, *Nelumbium* signalizes its distinction from the other *Nymphæaceæ* by the fact that the first leaf is not acicular, but it and the succeeding leaves closely resemble in miniature those of the mature plant.

Anatomy of the Mature Rhizome.

The chief feature in the structure of the rhizomes of the *Nymphæaceæ* is the astelic arrangement of their vascular bundles, and in most cases a second very prominent characteristic is occasioned by the almost indescribable confusion and complexity presented by these bundles in consequence of the exceedingly irregular courses they pursue and the intricate anastomoses they undergo. This complexity is found at its maximum in the rhizomes of *Victoria* and *Nymphæa*. The vascular bundles are for the most part massed together in the central region of the rhizome, where they run indiscriminately in all directions and without any attempt at order, the utmost diversity also being exhibited in their orientation. On the outside of this central region there lies a belt of continuous parenchyma comparatively free from vascular bundles, traversed only by those passing outwards from the central mass towards the exterior. Another narrow zone of tissue of exactly the same nature lies immediately below the surface of the rhizome. Finally, between these two there is a broad belt of "cavernous tissue" (*cf.* Henfrey, Phil. Trans., 1852, pp. 289–294). The latter is formed by a number of large lacunæ filled up with spongy masses of very loosely packed cells, and separated from each other by supporting plates or laminæ of continuous tissue connected on either side with the previously mentioned zones of firm parenchyma.

Those species in which the rhizomes remain throughout comparatively small, such as *Nymphæa flava*, show, in accordance with the diminution in the number of bundles present, a corresponding decrease in the complexity of their arrangement. Further, in this species and in *N. tuberosa* it is noticeable that almost all the inner bundles are oriented in the same direction, *i. e.* inversely; many of them having their xylems confluent with those of the outer normally oriented bundles. Differences are in

particular to be observed in the sharpness of the delimitation between the central vascular region and that surrounding it, although in no case is any appearance presented that might be regarded as a central cylinder. This distinction is least apparent in the Nymphæas, indeed it is scarcely to be observed at all in *N. alba* and *N. blanda*; whereas in *Victoria regia* it is very clearly defined, owing to the fact that the vascular elements at the periphery of the central mass constantly run in certain definite directions, forming thus a zone continuous but for interruptions due to the outward passage of traces to the leaves &c. The outer components of this peripheral zone are found to be groups of phloem elements running around the central region in obliquely horizontal directions, like so many hoops or girdles. Next within come a number of more or less separate vascular bundles (or sometimes groups of tracheides only), the elements of which run almost vertically. Finally, there is often another inmost system of tracheides running almost horizontally, although this last is frequently absent.

The rhizomes of the Nuphars differ from those of the Nymphæas, and from that of *Victoria regia*, principally in the absence of that "cavernous zone" described above. On the contrary, the ground-tissue is homogeneous throughout, and consists of a spongy lacunar parenchyma with large intercellular spaces which decrease in size as the periphery is approached. Again, the vascular bundles are not so confused; a greater proportion of them run vertically, especially in the peripheral regions, where certain of them are arranged in a very irregular ring, on the outside of which the ground-tissue is traversed by the small leaf-traces only. Most of the vascular bundles have their xylems turned towards the centre, although some are turned in various other directions. Some again run singly and separately in the ground-tissue, but the majority are fused together by their confluent xylems into groups of from two to four. These groups are due to the fact that the bundles in the course of their anastomosis very often run together and very closely applied to each other for some time before separating again.

In *Cabomba aquatica*, whether in the comparatively short internodes of the sympodial rhizome or in the elongated ones of the floating shoots, the structure, on account of its great simplicity, is very different in appearance from that described in the above genera. There are only two pairs of bundles present. In the rhizome the bundles of each pair are situated almost exactly facing each other; in the floating shoot each is placed along one arm of a **V**, the apex of which is occupied by a canal representing the disintegrated xylems of the pair. At every node a leaf-trace arises from each pair, being formed by the fusing together of two branches, one from each of the components of the pair. At the same time the two bundles of each pair separate and travel horizontally round the stem in opposite directions to meet the corresponding bundles from the other pair, with which they fuse to form the two pairs for the next internode.

With regard to *Nelumbium speciosum*, the rhizome possesses, in its elongated internodes, a large number of vascular bundles arranged in several concentric circles and running quite vertically. They are all directly oriented, except the members of the third and fifth inmost circles, which are all inverse. In the outer circles the bundles are undoubtedly free and separate from each other, but the twelve which form the inmost rings of all are held by Van Tieghem to constitute a central cylinder surrounded by a

common endodermis *, although this could not be decided from the young seedlings examined by me. In the nodal regions, which, according to Trécul †, represent four successive nodes with their internodes contracted to obliteration, the bundles of the two inmost circles branch and anastomose in an extremely complicated manner, as has been described by Wigand in the 'Bibliotheca Botanica,' vol. ii. Heft 11.

It seems to me possible that the intense complexity of the arrangement of the bundles in *Victoria*, *Nymphæa*, and *Nuphar* may have been derived from a simpler structure previously existent in a stem with longer internodes, as a result of the contraction and elimination of these internodes in consequence of the adoption by the stem of a rhizomic habit.

Anatomy of the Seedling.

The arrangement of the vascular tissue in the young seedling of *Victoria regia* is, on the whole, very similar to that in the mature rhizome, but the limiting zone of the central mass is more prominent, and is separated off from the irregular bundles lying within it in a much more decided manner, because the position of the inmost system of horizontal tracheides which are usually present in the mature rhizome is here occupied by a corresponding belt of parenchymatous cells. It becomes quite clear in the seedling that the bundles which supply the leaf-traces are derived from the internal vascular mass, whereas those which eventually supply the roots are derived from the limiting peripheral zone. Passing further down still in the seedling stem the central mass decreases steadily in size, particularly with regard to its internal irregular constituents, so that the bundles of the peripheral zone become relatively more conspicuous still. Nevertheless these also decrease in number until a point near the insertion of the first leaf is reached where only four of them remain. At this point also only a few of the tracheides of the internal vascular tissue persist. Finally the four peripheral bundles unite to form two, which are placed in the epicotyl exactly opposite one another, so that their xylems are confluent in the centre with the remains of the internal tracheides, if, indeed, any of these are still present. Stating these facts from another point of view, it may be said that the transition from the narrow epicotyledonary stele to the structure found in the mature stem takes place in *Victoria* in a manner quite similar to the same proceeding in an ordinary monostelic plant. The bundles of the epicotyledonary stele subdivide so as to form a number arranged in a ring around a central pith. So, for some time at any rate, the young seedling is undoubtedly monostelic, having a single central cylinder with a common endodermis surrounding it; the presence of the latter being, under suitable treatment, clearly demonstrable even so far up as the fourth leaf. But in *Victoria regia*, above the insertion of the first leaf, this central cylinder at the same time undergoes great modifications from the appearance in the medulla of an ever-increasing amount of vascular tissue. Concurrently with this the central cylinder itself becomes more and more expanded, irregular, and broken up, until in the mature rhizome its limits are quite unrecognizable as such.

* Bull. Soc. Bot. de Fr., vol. xxxiii. p. 75.

† Ann. des Sc. Nat., sér. 4, tom. i. p. 296.

The seedling of *Nymphæa zanzibariensis* also is at first monostelic, and for about the same distance upwards as in *Victoria regia,* but the transition from the stele of the epicotyl into that of the internode immediately above takes place in a different manner. The epicotyledonary stele is exactly similar to that of *Victoria,* and the two bundles which it contains as they pass upwards increase in size and subdivide; however, the several bundles thus formed do not separate from one another, but remain with their xylems confluent. Hence, although there is for a time a single central cylinder with a common endodermis, the bundles do not become distinct and arranged in a ring around a medullary region as they do in *Victoria.* Therefore the central cylinder must always be very slender, and any further extension to meet the increase in diameter of the stem has to be provided for by a complete separation of the bundles. This will also account for the absence of a peripheral zone around the central vascular mass in the mature rhizome of this genus.

The structure of the seedling of *Nelumbium speciosum* is widely different from those of *Victoria* and *Nymphæa,* and is particularly remarkable for the large number of vascular bundles exhibited in the epicotyledonary internode. There are some 20–30 of them arranged in concentric circles, much as in the internodes of the mature rhizome, from which the chief differences are, that in the epicotyl the bundles are fewer, and that the two circles of inverse bundles are absent. The second internodal region has a structure almost identical with that of the mature rhizome.

It is a remarkable fact that in the seedling of *Nelumbium* an almost complete absence of primitive features is met with both in the leaves and in the stem. Moreover, the primary root is completely abortive and never escapes from the seed-coat. The precocity with which this plant assumes its definitive form stands in strong contrast to the gradually progressive stages exhibited by the other members of the order.

Apical Meristem.

I have not been able to obtain preparations of the apex of a mature plant of *Victoria regia,* but microtome series of that of *Nymphæa tuberosa,* prepared by Dr. Scott, show clearly that the apical cone is entirely composed of a number of homogeneous meristematic cells, no desmogen strands appearing therein until considerably lower down, where they are developed in an entirely indiscriminate manner. Nothing resembling a plerome is at any time to be discovered. I have also found a very similar state of affairs in *Cabomba aquatica.* The apex of the floating shoot has the form of a small rounded cone composed of rather large meristematic cells, among which no sort of differentiation is exhibited, until, at a point lower down, the procambial rudiments of the two vascular strands appear on opposite sides of the stem.

On the other hand, in the young seedlings of *Victoria regia* and of *Nymphæa zanzibariensis,* taken while yet barely out of their monostelic stage (Pl. XXI. fig. 9), the meristematic tissue of the apical cone itself is continued down into the stem as a central column or cylinder of very similar meristematic cells, in which, later on, desmogen strands make their appearance. In the case of the *Nymphæa* they are irregularly scattered throughout it; in *Victoria* those situated at the periphery seem to be the first developed.

So that, although there is no separation of plerome and periblem in the apical cone itself, a little lower down in the young stem such a distinction becomes evident.

Insertion of the Adventitious Roots.

In the several genera examined by me, and probably throughout the whole order, the rhizomes are beset with adventitious roots springing in clusters from the bases of the petioles. In *Nelumbium* they are present at the base of every leaf, so also, the first or acicular leaf excepted, in *Victoria*, *Nymphæa*, and *Nuphar*. The number of roots belonging to each cluster varies considerably, being greatest (15–20) in the mature rhizome of *Victoria* (Pl. XXI. fig. 10); on the other hand, in *Nymphæa* and *Nuphar* each group contains from 3 to 7 only.

These roots are given off from certain vascular bundles especially set aside for that sole purpose, which are separated off from the central vascular mass, and run apart from it in an upward direction in the outer region of the rhizome into the dorsally protuberant bases of the petioles, where they lie on the outer side of the leaf-traces (fig. 11).

That certain bundles were thus set aside for the express purpose of bearing the adventitious roots was observed by Trécul in *Nuphar luteum* in 1845 *, in *Victoria regia* by Henfrey in 1852 †, and in *Nelumbium speciosum* by Wigand in 1871 ‡. I have further discovered that the different species show interesting variations in the manner in which these bundles are arranged. For instance, in *Victoria regia* (fig. 12) all the root-bearing bundles belonging to the same leaf-base are grouped together so as to form a structure having the appearance of a definite and distinct stele, consisting of a number of vascular bundles, usually about 20, arranged in a complete ring, with the phloem groups well marked and generally distinct from each other, while the xylem elements form a more or less continuous ring within them. Other xylem elements are scattered throughout the central parenchyma of the stele, so that no definite medulla is distinguishable (fig. 13). The xylem is centrifugally developed, although, since it is entirely composed of long pointed tracheides, longitudinal sections are necessary to settle this point. The whole stele is surrounded by a clearly marked endodermis. This stele bears the adventitious roots in acropetal succession on its outer side, while it itself terminates in the youngest root or roots.

Owing to the delay in the further development of the adventitious roots after their first formation they possess pedicels of a considerable length, and do not obtain individual cortices until they have reached the extreme periphery of the leaf-base, where the point at which they do so is marked in each root by the presence of a hemispherical transverse diaphragm formed by a layer of small closely packed cells. These diaphragms enable the roots to be broken off the stem, leaving behind a clean-cut scar and not a tear. In appearance the pedicels resemble the structure of a stem stele much more than that of a root (fig. 14). They have a ring of several indistinct groups of phloem, and within this an almost continuous ring of xylem elements surrounding a small medulla; the whole

* Ann. des Sc. Nat., sér. 3, tome i. p. 293 *et seq.*

† Phil. Trans. 1852, p. 289 *et seq.*

‡ Botanische Zeitung, No. 48, p. 821.

appearing perfectly collateral. However, at the point where the root first obtains its individual cortex, groups of small xylem elements are seen lying *between* the phloems, and at the same time the xylem *underlying* the phloems disappears, so that at this point the typical root-cylinder is established. In *Nymphæa,* where the roots are fewer to each cluster, the root-bearing stele is smaller and more irregular than in *Victoria,* it is also considerably shorter. It runs at first almost horizontally outwards, and does not turn upwards until it has given off the first, *i.e.* lowest root. The pedicels here attain the appearance of a normal root cylinder shortly after they leave the root-bearing stele and before they possess individual cortices. In perfection of structure the stele formed by the root-bearing bundles varies with the species. Thus, in *Nymphæa alba* and *N. tuberosa* the 10–12 vascular bundles are arranged throughout their course in a complete and well-formed stele, essentially similar in all points to that of *Victoria regia.* In *N. flava* the stele is much smaller, containing about 6 or 7 bundles only, and it is at the same time to a certain extent incomplete, for the phloem groups are very scanty or altogether wanting on the inner side, especially in the lower portion of the stele. In *N. blanda* a stele, as such, can scarcely be said to exist at all, the several root-bearing bundles pass out from the central mass distinct and separate from each other. They become arranged in a semicircle, and later fuse up laterally to form a continuous arc, finally to form a more or less imperfect stele as in *N. flava.* In this respect *Nymphæa blanda* makes a close approach to the condition observed in the Nuphars (*N. advena* and *N. luteum*), where the root-bearing bundles, some 10 in number, also pass out from the central vascular mass separately, and very soon fuse together into an irregular band or arc of greater or less curvature, sometimes almost a complete circle. A segment of this arc becomes separated off to supply the first or lowest root; the ends of this smaller arc immediately grow round to meet each other, and form thus a complete ring, so that the pedicel has at its base the strange appearance of a ring of vascular bundles surrounding a pseudomedullary mass of ground-tissue with both an external and an internal endodermis. This structure is retained even after the vascular bundles have taken up the radial arrangement typical for a root stele, which they do long before the root attains a cortex of its own. As the pedicel contracts to form the narrower cylinder of the root itself, the pseudomedullary tissue and the internal endodermis gradually disappear. After the departure of a root the remaining portions of the arc of root-bearing bundles either fuse up again as before, or form separate groups until the next root is to be given off, when the same proceeding is repeated.

In *Cabomba* and *Nelumbium* the rhizomes bear adventitious roots in the same manner at the nodal regions on special steles, which pass directly outwards, but only reach a short distance before they break up into an umbel of roots all springing from about the same point.

In *Cabomba aquatica* it appears that only the sympodial rhizome bears roots: the floating shoots bear no roots at all. The comparatively stout stele is very short, and consists of a mass of xylem elements scattered in the central conjunctive tissue, and surrounded by a narrow ring of phloem, in which separate bundles can hardly be distinguished.

The Occurrence of Polystely.

During the progress of these investigations my attention was directed by the Curator of the Gardens, Mr. Watson, to certain remarkably elongated stolons or runners borne laterally on the rhizomes of *Nymphæa flava.* They are found below the surface of the soil, and are evidently produced in order to ensure the survival of the plant through those seasons of the year which are unfavourable to its continued growth, and at the same time to increase the number of individuals. Similar functions are performed by the laterally produced tubers in *Nymphæa tuberosa.*

The stolons of *N. flava* attain a considerable length (30–40 cm.), and are slightly thickened at their terminations, where they bear a number of short tuberous starch-laden roots on their under surface, and on their upper surface a number of buds protected by scale-leaves (Pl. XXII. fig. 15). In these stolons the vascular bundles are arranged in 4–5 widely separated groups lying in a uniformly lacunar ground-tissue, with a rather abruptly marked off hypodermal zone of continuous parenchyma (fig. 16). Each group consists of 3–4 vascular bundles arranged around a central canal which has taken the place of their disintegrated protoxylems, the remains of which are still to be seen at the borders of the lacuna. The phloem groups, on the other hand, are well developed and very prominent; seen in transverse section they are ovate in outline and quite distinct from each other. In greater part they are composed of sieve-tubes of exceptionally large lumen accompanied by their companion cells, while on the outside there is a small cap of phloem parenchyma. Only a few of the later formed elements of the xylem are persistent on the inner side of the phloem groups; they are separated by several parenchymatous cells from the central canal. At either end of the runner this xylem is considerably increased in amount, and its elements fill up the space elsewhere occupied by the canal. A beautifully-marked endodermis surrounds each group completely; so that each of them exhibits in itself all the essentials of a complete stele (fig. 17). It is curious to note that in the cells of the endodermis the fold on the radial walls is rarely placed exactly in the centre, but is nearly always situated nearer to the inner tangential wall than to the outer—an idiosyncrasy which is also a characteristic of the polystelic Primulas and Gunneras. Approaching the termination of the runner where the buds and tuberous roots are borne, the ground-tissue becomes continuous throughout, the lacunæ disappearing; the bundles in each stele become confused and indistinct; and at certain intervals, in relation to the insertion of the buds, the steles themselves fuse up into an irregular circle, beyond which they scarcely regain their identity before they enter into another similar fusion, and so on.

In *N. tuberosa* the stalks which bear the tubers are very short, not more than 4 cm. long, some of the tubers being almost sessile. Their structure in all cases examined is essentially similar to that of the runners of *N. flava,* 3–5 separate steles being present, each composed of 3–5 vascular bundles, although here the ground-tissue is without lacunæ, and the bundles within each stele are less distinctly separated from one another. The whole structure is, in fact, closely comparable to that of the runners of *N. flava* near their tuberous bud-bearing extremities.

In all cases where tubers are produced in the *Nymphæaceæ* the first or first two internodes of the new growth resulting from their germination develop into thin stolons, in *Nymphæa flava* about 5 cm. long, which swell out at their extremities to form new rhizomes (Pl. XXII. fig. 18). And it is a very remarkable fact that the first leaves borne on these rhizomes are submerged ones, entirely similar to the embryonic leaves of the young seedling, except that the very first leaf of all is not truly acicular, but possesses a very small lamina.

When these new growths arise from buds upon a primary runner or stolon, as in *N. flava*, they may be called secondary stolons. They contain 4–7 vascular bundles (in fig. 19, 4 only), and the exact manner in which they are arranged varies from one stolon to another, and even in the different regions of the same stolon; thus, a varying number of them may be united in pairs, or they may be all separate and distinct. In fig. 19 there are two separate bundles, and two fused to form a pair. Sometimes six bundles are present, and these are fused together so as to form two pairs; then the resemblance that such a section bears to one of the floral peduncles of *Cabomba aquatica* is most remarkable, for here also there are six bundles almost identical in appearance, and also united into three pairs. The vascular bundles of the secondary stolon are exactly similar to those described in the primary. The phloem groups are very prominent, with an outer cap of phloem parenchyma, within this a mass of large sieve-tubes with their companion cells, and then a few small xylem elements at their inmost points, the position of the earlier-formed elements being as before occupied by a canal formed by their disintegration; and finally each bundle or pair of bundles is surrounded by a very clear endodermis. As the runner approaches its termination, where it becomes converted into the new rhizome, it increases very much in girth, the internodes between the first leaves, which are borne at this point, being very short and thick. The vascular bundles, whether single or in pairs, increase in size, lose their regularity, and fuse laterally with each other. At the same time they subdivide so as to form so many groups of bundles which partially recover their identity after each node, although less and less distinctly as you pass higher up in the stem, until at last the usual structure of the rhizome is attained.

It is especially to be observed in some species that those rhizomes which take their origin in this manner from such secondary stolons have their vascular bundles, throughout the whole rhizome, more or less gathered into groups around different centres, generally three, forming groups which correspond to those found at the base. All the bundles in each group direct their xylems towards the point around which they are arranged; and so it comes to pass that in these rhizomes the inner bundles of the vascular mass are, for the most part, inversely oriented, which point has been previously referred to.

A similar grouping is seen in the tubers of *N. tuberosa*, which are borne on the polystelic stalks mentioned above.

Summary.

We see, therefore, that the plants in this Order, although generally astelic, sometimes aggregate all the vascular bundles present in certain of their members into so many steles, or, it may be, that only those bundles which are set apart for a certain function are thus dealt with, although they may be lying in a region of the plant otherwise astelic.

These steles vary greatly in compactness, size, and particularly in the number of bundles which assist in their formation. From the large many-bundled root-bearing steles of *Victoria regia*, through the smaller ones of about a dozen bundles of *Nymphæa alba* and *N. tuberosa*, we pass to the steles containing four to three only in the primary stolon of *N. flava*, and finally to those containing two bundles in the secondary stolons of the same plant and throughout the whole structure of *Cabomba* and *Brasenia*—if, indeed, we are entitled to call the latter steles at all. In relation to this point the close similarity that these paired bundles show in all points of structure to the pair of bundles found in the cylinder of the epicotyl of *Victoria* and *Nymphæa* should be borne in mind, and the latter, in virtue of its position, must be acknowledged as a diarch stele. Moreover, there are many other admitted steles which consist of two bundles only in the stems and petioles of many Ferns and Selaginellas. If this question be answered in the affirmative, *Cabomba* and *Brasenia* must no longer be described as astelic, but as essentially polystelic. However, the exact manner in which the two pairs arise from the central cylinder of the epicotyl should first be determined before any final decision is arrived at.

Finally it may be remarked that the simplicity of the anatomical structure in *Cabomba* and *Brasenia* is completely in accordance with the structure of their flowers, the want of complexity in which also distinguishes these plants from the rest of the Order—the parts of the flower being arranged in whorls of three only, and the gynæcium being superior and apocarpous.

EXPLANATION OF THE PLATES.

Plate XXI.

Figs. 1–4. Young stages of mature leaves of *Victoria regia*. 1. Very young, front view (×10). 2. Older, back view (×8). 3. Still older, side view (×8). 4. Young leaf, *in situ*, seen from behind, and showing axillary scale, which curves away from the leaf (× about 2).

Fig. 5. Young stage of mature leaf of *Nymphæa zanzibariensis*, showing the free lateral stipules (×4).

Figs. 6–8. Embryonic leaves of *Victoria regia* seedling (nat. size). 6. 3rd leaf showing the "pocket" of the lamina at the insertion of the petiole. 7. 4th leaf, front view. 8. 4th leaf, back view.

Fig. 9. Median longitudinal section of apical region of young seedling of *Nymphæa zanzibariensis*: *lt.*, leaf-trace; *rt.*, root-bearing stele; *vv.*, desmogen strands in central meristematic cylinder (×240).

Figs. 10–11. Base of petiole of mature leaf of *Victoria regia* (nat. size). 10. In surface view, showing position of adventitious roots. 11. In section: *rt.*, root-bearing stele; *p.*, pedicels; *l.*, air-canals in the petiole.

Fig. 12. Transverse section of the root-bearing stele of same plant (×80): *x.*, xylem; *ph.*, phloem; *e.*, endodermis.

Fig. 13. Portion of such a stele, more highly magnified (×225).

Plate XXII.

Fig. 14. Transverse section of the pedicel of an adventitious root of *Victoria regia* taken near its point of origin from the root-bearing stele (×155).

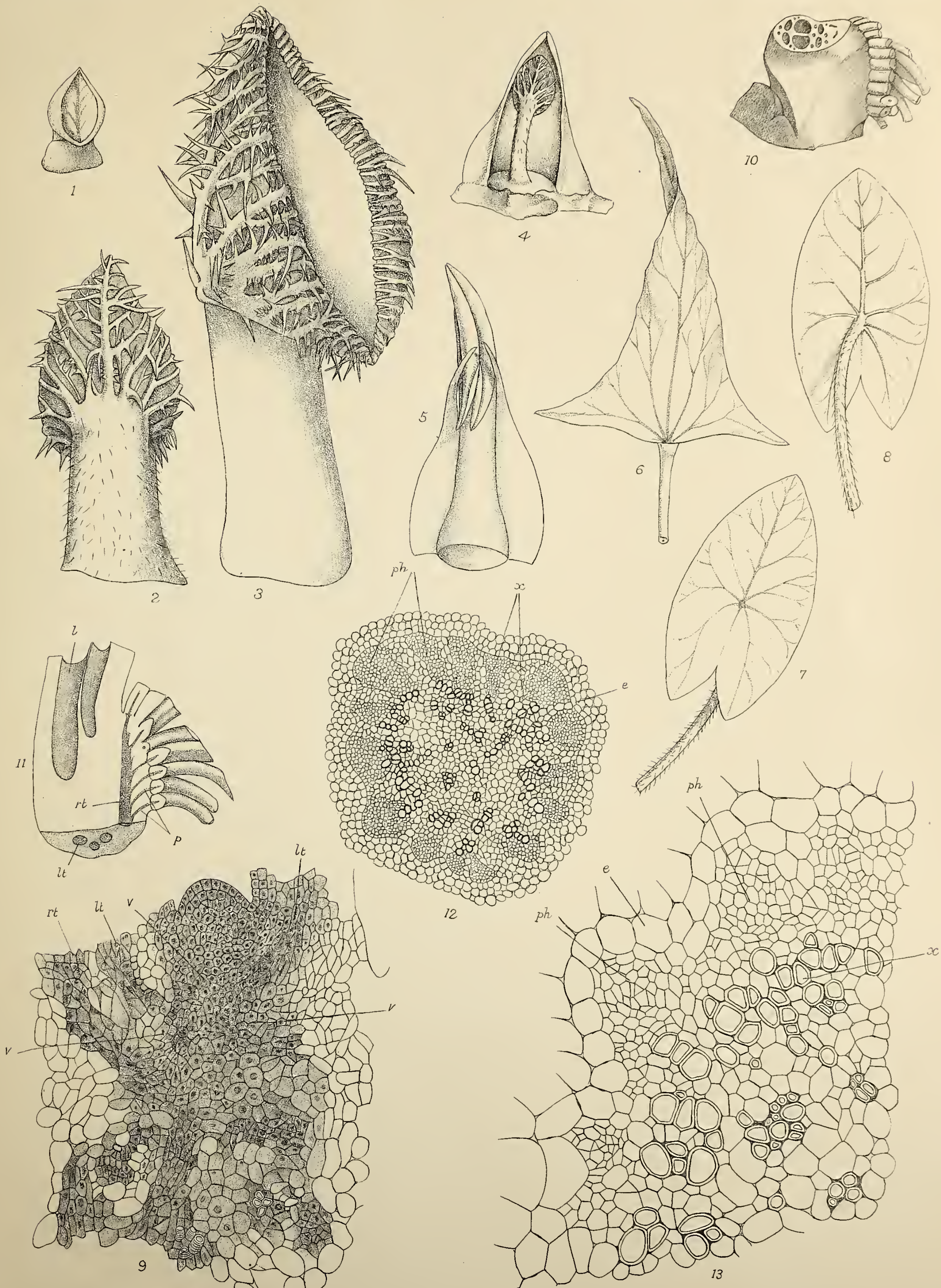
Fig. 15. Plant of *Nymphæa flava* ($\frac{2}{3}$ nat. size): *st.*, primary stolon, bearing buds, *b.*, and tuberous roots, *r.* The stolon becomes slightly tuberous during its course at point *p.*; *l.*, leaf-scars on rhizome.

Fig. 16. Transverse section of the primary stolon of the same plant, showing four steles, two with four bundles each, and two with three only (×25).

Fig. 17. Stele of the same, more highly magnified (×150): *x.*, persistent xylem-elements; *st.*, sieve-tubes; *p.*, phloem parenchyma; *e.*, endodermis; *l.*, central canal with remains of protoxylem; *h.*, stellate hair.

Fig. 18. Thickened extremity of primary stolon (slightly enlarged): *pr.st.*, primary stolon; *b.*, buds on the same. The oldest has grown out into the secondary stolon, *sc.st.* The latter thickens above to form the new rhizome, *rz.* $l.^1$, 1st leaf of new rhizome, $l.^2$, the second, $l.^3$, the third: *r.*, tuberous roots.

Fig. 19. Transverse section of secondary stolon (×30). Four vascular bundles present: *a* is a single separate one; *b* has been formed by the complete fusion of the two bundles of such a pair as that at *c*.



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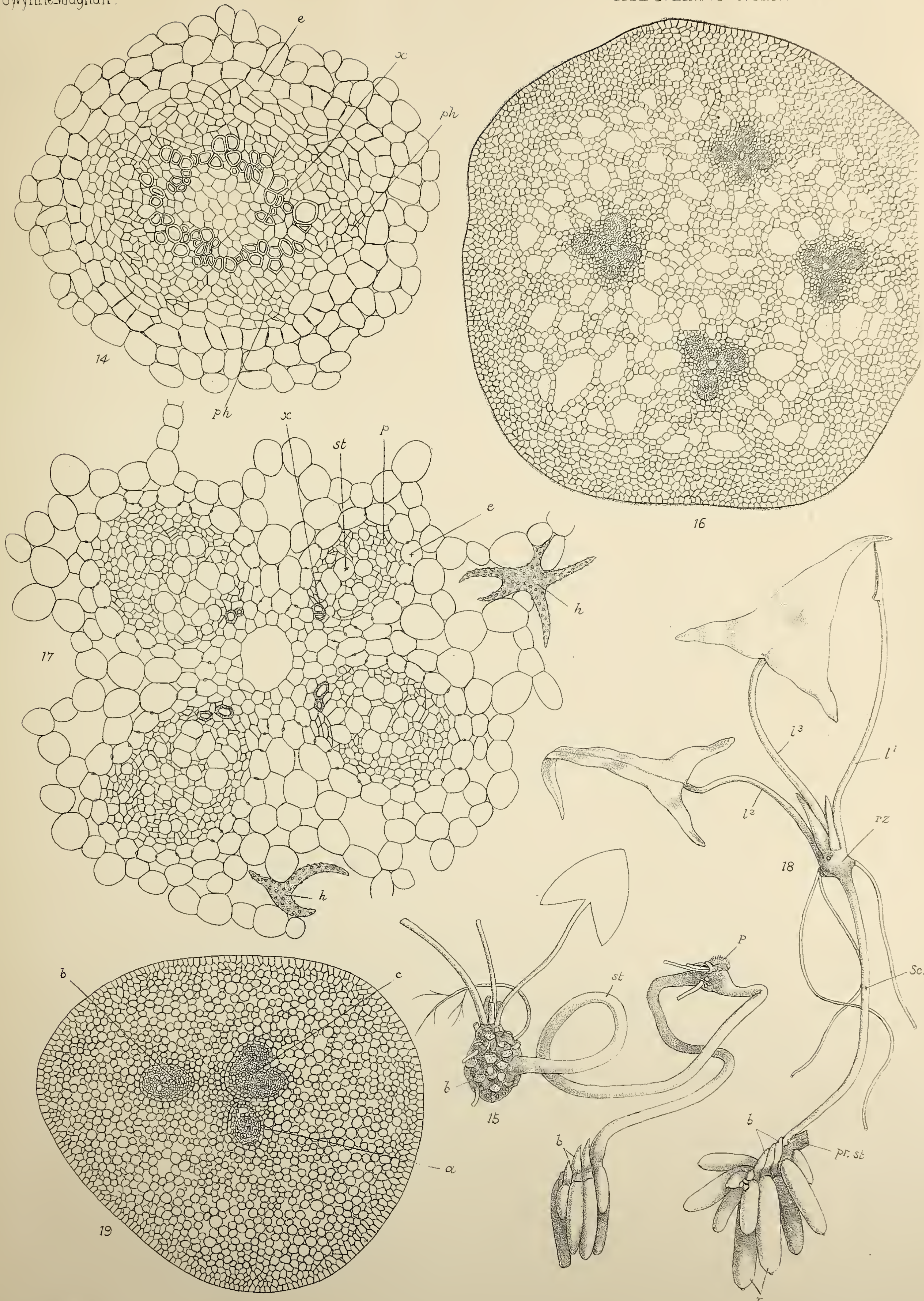

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